

# STUDIES ON THE REPRODUCTIVE SYSTEM OF *NIVENIA CORYMBOSA* (IRIDACEAE), AN APPARENTLY ANDRODIOECIOUS SPECIES<sup>1</sup>

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## ABSTRACT

*Nivenia corymbosa* has flowers with a stamen- and style-length dimorphism but pollen monomorphism. Results of an intra- and intermorph crossing program suggest that this species is androdioecious rather than conventionally distylous. A single progeny grown from a selfed long-styled plant contained 1:1 longs:shorts, suggesting that the longs of the ancestral distylous condition are the heterozygous morph rather than the homozygous one.

The small South African genus *Nivenia* is of interest because it is one of two genera of Iridaceae in which heterostyly has been reported (Ornduff, 1974).<sup>3</sup> Three species of this small woody genus are reportedly distylous with one morph having an exerted style and short stamens, and the other having exerted stamens and a short style. In *N. binata* Klatt, distyly is associated with pollen dimorphism as well (Mulcahy, 1965). At least three species of *Nivenia* are monomorphic with a floral morphology resembling that of the long-styled form of the distylous species (Ornduff, 1974). This paper presents the results of an artificial pollination program using the dimorphic *N. corymbosa* (Ker) Baker that was designed to determine the presence and nature of incompatibility in this species.

## MATERIALS AND METHODS

The crossing program utilized four field-collected short-styled plants of *N. corymbosa* and one short- and four long-styled plants derived by selfing a long-styled plant. The terms "long" and "short" will be used in this paper to refer to these two morphs, but in view of the apparent androdioecism of this species, they are not equivalent to the usage of "pin" and "thrum" of distylous species. The material originated from Bains Kloof, Cape Province, South Africa (Ornduff 7666, UC). Plants were grown in an insect-free greenhouse in Berkeley and pollinations were made using fine-tipped forceps. Self-, intramorph, and intermorph pollinations were carried out, and as controls some flowers were left unpollinated and

others were emasculated. One long-styled plant was selfed and the style length of the progeny scored. As capsules matured, they were placed in seed packets and the number of seeds was counted at the end of the program. Pollen viability, size, and wall sculpturing were determined using pollen grains from two plants of each morph mounted in aniline blue-lactophenol or lactophenol.

## RESULTS

The pollen viabilities of the field-collected plants ranged from 92 to 100 percent and of the progeny grown from seed from 56 to 95 percent. Pollen size was monomorphic: for two longs  $\bar{X}$  37.7  $\mu\text{m}$  ( $\sigma = 1.8$ ) and 37.3  $\mu\text{m}$  ( $\sigma = 2.2$ ) and for two shorts  $\bar{X}$  37.7  $\mu\text{m}$  ( $\sigma = 1.8$ ) and 41.4  $\mu\text{m}$  ( $\sigma = 2.1$ ). Wall sculpturing was also monomorphic.

None of the emasculated or intact control flowers produced seeds (Table 1). Self-pollinations of shorts produced no seeds and of longs produced an average of 0.04 seeds per pollination. Intramorph pollinations of shorts and longs produced an average of 0.2 seeds per pollination. Intermorph pollinations of shorts as seed parents produced an average of 0.3 seeds per pollination and of longs as seed parents 3.4 seeds per pollination. The single progeny grown from a selfed long contained 6 longs and 6 shorts.

## DISCUSSION

The presence of an incompatibility system in *Nivenia corymbosa* is evidenced by the lower seed set following intramorph pollinations compared

<sup>1</sup> Supported in part by grants from the National Science Foundation and the Committee on Research, University of California, Berkeley.

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<sup>3</sup> The other genus for which heterostyly has been reported is *Geissorhiza*, in which plants of some populations of *G. heterostyla* L. Bolus have dimorphic flowers that are not conventionally distylous (Ornduff, 1974).



TABLE 1. Results of intramorph and intermorph pollinations of *Nivenia corymbosa*.

| Cross <sup>1</sup>             | Number<br>Flowers<br>Uti-<br>lized | Num-<br>ber<br>Cap-<br>sules<br>Produced | Num-<br>ber<br>Seeds<br>Pro-<br>duced | Number<br>Seeds<br>per<br>Polli-<br>nation |
|--------------------------------|------------------------------------|--|---------------------------------------|--|
| Controls:                      |                                    |  |                                       |  |
| SP1 (intact,<br>unpoll.)       | 11                                 | 0  | 0                                     | 0  |
| LP2 (intact,<br>unpoll.)       | 21                                 | 0  | 0                                     | 0  |
| LP2 (emasc.,<br>unpoll.)       | 18                                 | 0  | 0                                     | 0  |
| LP3 (intact,<br>unpoll.)       | 16                                 | 0  | 0                                     | 0  |
| Self-pollinations:             |                                    |  |                                       |  |
| SF1                            | 49                                 | 0  | 0                                     | 0  |
| SF2                            | 69                                 | 0  | 0                                     | 0  |
| SF3                            | 92                                 | 0  | 0                                     | 0  |
| SF4                            | 56                                 | 0  | 0                                     | 0  |
| LP2                            | 52                                 | 1  | 3                                     | 0.06                                       |
| LP4                            | 15                                 | 0  | 0                                     | 0  |
| Intramorph cross-pollinations: |                                    |  |                                       |  |
| SF1 × SF2                      | 14                                 | 5  | 26                                    | 1.9  |
| × SF3                          | 23                                 | 0  | 0                                     | 0  |
| SF2 × SF3                      | 26                                 | 0  | 0                                     | 0  |
| SF4 × SP1                      | 55                                 | 5  | 5                                     | 0.09                                       |
| SP1 × SF4                      | 28                                 | 5  | 2                                     | 0.07                                       |
| LP3 × LP2                      | 53                                 | 3  | 9                                     | 0.2  |
| Intermorph pollinations:       |                                    |  |                                       |  |
| SF4 × LP2                      | 59                                 | 8  | 22                                    | 0.37                                       |
| SP1 × LP2                      | 29                                 | 4  | 3                                     | 0.1  |
| LP1 × SF4                      | 56                                 | 21                                       | 230                                   | 4.1  |
| LP2 × SF1                      | 1                                  | 1  | 4                                     | 4.0  |
| × SF4                          | 41                                 | 20                                       | 115                                   | 2.8  |
| LP3 × SF4                      | 31                                 | 12                                       | 87                                    | 2.8  |

<sup>1</sup> Code numbers of individual plants are used: F = field-collected plant, P = progeny of selfed field-collected plant; L = long, S = short.

with that following intermorph pollinations of pins. However, the average seed production of shorts following intermorph pollinations is approximately equal to that following intramorph pollinations and does not exceed 5 percent of the average maximum seed set of longs. The pollen viability of one short used as a seed parent in an intermorph cross was reduced (69 percent) but in the other individual it was high (97 percent), so the low fecundity of these crosses probably should not be attributed to gametic sterility fac-

tors. It is also possible that this difference in seed set between the two morphs is attributable to mechanical problems in depositing sufficient pollen grains on short stigmas. This does not seem to be a likely explanation for these differences, since observations of pollen loads on naturally-pollinated stigmas of *N. binata* (a species with a floral morphology very similar to that of *N. corymbosa*) collected at Swartberg Pass, Cape Province, indicated an average number of 33.3 pollen grains on long stigmas and 27.8 pollen grains on short stigmas (with no attempt to discriminate visually between intra- and intermorph pollen grains; Ornduff, pers. obs.). If such figures are a measure of normal stigmatic pollen loads carried by fecund individuals of the distylous *N. binata* in the field, the number of compatible pollen grains per stigma required for modal seed set of both longs and shorts is very low and would likely be deposited on stigmas via artificial pollinations. A third possible explanation of the observed seed set in *N. corymbosa* is that the species is essentially androdioecious, that is, some individuals produce perfect flowers and others produce staminate flowers. The data at hand, including the occurrence of pollen monomorphism in this species, are compatible with this suggestion. That some shorts occasionally produce small numbers of seeds suggests that androdioecism is not fully developed in this species.

Various types of reproductive systems involving a sexual separation have evolved from heterostyly in other groups. These include full dioecism in some members of the Rubiaceae and Menyanthaceae and androdioecism in *Oxalis suksdorfii* (see Ganders, 1979). That various modifications of the distylous breeding system have evolved elsewhere in *Nivenia* is evidenced by the occurrence of long-styled monomorphism in at least three species with apparent associated self-compatibility in *N. stokoei* (Guthrie) N. E. Brown (Ornduff, 1974). The 2:1 rather than 1:1 long:short morph ratio of a field population of the distylous *N. binata* also suggests that the breeding system of this species may deviate from that expected for a conventional distylous species (Ornduff, 1974).

It is of interest to note that the progeny of a selfed long-styled plant of *Nivenia corymbosa* produced a 1:1 ratio of longs to shorts. Assuming that the androdioecism of this species is derived from a more conventional distylous ancestral condition, this suggests the possibility that in *Nivenia* longs are the heterozygous genotype, a



condition otherwise known for certain in the distylous *Hypericum aegypticum* (Ornduff, 1979) and also possibly in the dimorphic *Armeria maritima* (Baker, 1966). For those interested in the comparative evolution of breeding systems and in the selective forces that lead to the breakdown of heterostyly, *Nivenia* clearly merits further attention and field studies are particularly needed.

#### LITERATURE CITED

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